The effect of stem density on the probability of attack by the ambrosia beetle

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Title

The effect of stem density on the probability of attack by the ambrosia beetle *Platypus quercivorus* varies with spatial scale

Running title

Stem density affects beetles' attack probability

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Abstract

1. The ambrosia beetle, *Platypus quercivorus*, uses fagaceous tree species as its hosts, and causes Japanese oak wilt by transporting and introducing the pathogenic fungus *Raffaelea quercivora* into the host tree. It is necessary to understand the host selection process used by the beetle in heterogeneous forests in order to protect fagaceous trees.
2. The occurrence of beetle attack on *Quercus crispula* and *Castanea crenata* was monitored from 2008 to 2011 in two 1-ha and one 0.5-ha plots established in a secondary forest. The stem and crown densities of each fagaceous tree species were calculated at 11 different spatial scales for each individual tree. Model application and selection were performed to clarify factors affecting the probability of attack by *P. quercivorus*.
3. As shown in previous studies, a higher probability of attack was predicted for *Q. crispula* than for *C. crenata*, and the predicted probability of attack was lower for trees attacked in the previous year.
4. The effect of stem density on the probability of attack was positive at a small (5-m radius) spatial scale, and negative at larger (5- to 17.5-m radius) scales. We interpreted this to indicate that a dense distribution of fagaceous trees in a small area had a higher probability of attack, and that this probability decreased with increasing density of fagaceous trees in a surrounding concentric area.
5. A positive effect of crown density was detected, suggesting that *P. quercivorus* has a means of detecting host trees in areas with high crown densities of fagaceous species.

Keywords

Castanea crenata, generalized linear mixed model, host selection, Japanese oak wilt, *Quercus crispula*

Introduction

Ambrosia and bark beetles are secondary insect pests that attack weakened trees as their hosts (Wood, 1982). Some species of these beetles can become primary insect pests and may begin to attack healthy trees when their populations reach epidemic size (Rudinsky, 1962), which can cause extensive damage to forests. In recent years, wilt diseases in trees caused by pathogenic fungi of the genus *Raffaelea* have been reported worldwide; the vectors of these fungi are ambrosia beetles. For example, *Platypus cylindrus* attacks *Quercus suber* in Europe (Henriques *et al.*, 2006), *P. koryoensis* attacks *Q. mongolica* in Korea (Hong *et al.*, 2006), *Megaplatypus mutatus* attacks poplars (*Populus* spp.) and willows (*Salix* spp.) in Argentina (Alfaro *et al.*, 2007), and *Xyleborus glabratus* attacks redbay (*Persea borbonia*) in the USA (Fraedrich *et al.*, 2008).

In Japan, the ambrosia beetle *Platypus quercivorus* vectors the pathogenic fungus *Raffaelea quercivora* from dead to healthy trees (Saito *et al.*, 2001; Kinuura & Kobayashi, 2006), and causes Japanese oak wilt (Ito *et al.*, 1998; Kubono & Ito, 2002). This beetle was originally thought to be a secondary pest that used weakened fagaceous trees as its hosts in sporadic outbreaks (Ito & Yamada, 1998). However, in the 1980s, *P. quercivorus* became a primary pest and began to attack healthy trees in several districts of Japan (Ito & Yamada, 1998). These epidemic populations have gradually dispersed and mixed with local populations (Shoda-Kagaya *et al.*, 2010), and the areas in which fagaceous trees have been damaged continue to expand (Kobayashi & Ueda, 2005).

In *P. quercivorus*, males are responsible for host selection. The mating system of Platypodidae, the family to which *P. quercivorus* belongs, exhibits male-initiated monogamy (Kirkendall, 1983); male beetles first fly to their host trees, into which they bore holes. The chemicals involved in the initial attack by *P. quercivorus* are as yet unknown. Male *P. quercivorus* that initially attack trees produce the aggregation pheromone quercivorol, ((1*S*,4*R*)-*p*-menth-2-en-1-ol, Kashiwagi *et al.*, 2006), to attract conspecifics, and males and females attracted by the pheromone attack trees *en masse* (mass attack, Ueda & Kobayashi, 2001). Female beetles extend galleries into the sapwood where they inoculate the symbiotic fungus onto the gallery walls and oviposit eggs. Hatched larvae grow inside the gallery and emerge from holes after approximately

1 year. Survivorship of larvae is highly dependent on the suitability of the tree selected by the males.

Within a forest of many host and non-host tree species, individual male *P. quercivorus* select one host tree and bore into it. Male *P. quercivorus* that were artificially introduced into logs were also shown to bore holes into non-host tree species; they excavated holes in both host (*Quercus crispula*, *Q. serrata*, and *Castanea crenata*) and non-host (*Sorbus japonica* and *Cryptomeria japonica*) tree species (Tarno *et al.*, 2011). This behavior is non-adaptive, because reproductive failure occurs in beetles that excavate holes in non-host tree species. Therefore, in natural conditions, *P. quercivorus* must select a suitable host tree prior to boring holes. Previous studies have indicated that the insect rejects trees with a previous infestation history (Yamasaki & Futai, 2008), and that it prefers *Q. crispula* over *Q. serrata* and *C. crenata* (Yamasaki & Futai, 2012). In addition to infestation history and species, tree size is an important parameter for *P. quercivorus*: it prefers thicker trees over thinner trees (Akaishi *et al.*, 2006; Yamasaki & Sakimoto, 2009). It has been suggested that this preference is due to the larger volume of sapwood available in thicker trees for constructing galleries (Hijii *et al.*, 1991).

The density of host tree species is also an important factor affecting the host selection process of *P. quercivorus*. A positive effect of host tree (*Q. crispula*) density on the probability of attack by *P. quercivorus* was shown in a forest with a clumped distribution of host tree species; *P. quercivorus* preferred clumped trees over isolated trees (Yamasaki & Sakimoto, 2009). In a forest dominated by the host tree species, however, it is also possible that the density of the host could reduce the probability of attack by *P. quercivorus*. In animals, individuals form groups to reduce their own risk of being attack (Williams, 1966; Hamilton, 1971). Regarding host trees that are densely distributed in a wide range of forest as aggregated “prey,” this “dilution effect” might cause a decrease in the probability of attack of an individual tree by the “predator” *P. quercivorus*. Therefore, the density of host tree species must be examined at multiple scales.

Topography indirectly affects the life cycle and behavior of beetles, and may also affect the probability of trees being attacked by the beetle. The probability of *Nothofagus cunninghamii* being attacked by *P. subgranosus* decreased with increasing

altitude, i.e., with decreasing temperature (Elliott *et al.*, 1987), and attacks by *I. confusus* occurred in low-elevation stands on steeper slopes where winds that were favorable for dispersal of the beetle occurred (Santos & Whitham, 2010). Although the elevation range in the subject area of our study was too narrow to produce a difference in temperature, the complex topography in this area may affect the host selection behavior of *P. quercivorus*.

Positive phototaxis has been demonstrated in *P. quercivorus* (Igeta *et al.*, 2003), which suggests that the beetles fly upwards after their emergence toward canopy gaps created by dead trees. In addition, flying *P. quercivorus* were captured by balloon traps at heights of up to 16 m, although the number captured was very small (Igeta *et al.*, 2004). Assuming that *P. quercivorus* approaches its host trees from above rather than from below, crown density is another factor that may help the beetle to determine its attack target. In conifer-inhabiting bark beetles, green leaf volatiles (GLV) were demonstrated to be the key to rejection of non-host tree species (Schlyter & Birgersson, 1999; Zhang & Schlyter, 2004). If the opposite were true for *P. quercivorus*, which uses broad-leaved trees as its host, the potential to detect GLV could be greater near the canopy. In this context, the crown density of host trees immediately above the subject tree may be correlated with the probability of attack by the beetle.

In this study, we investigated attacks by *P. quercivorus* on *Q. crispula* and *C. crenata* in a secondary forest dominated by these two tree species. A generalized linear mixed model was constructed to predict the probability of a beetle attack occurring on a particular tree in a particular year, with tree species, basal area, previous infestation history, topography, stem density, and crown density of fagaceous trees as candidate explanatory variables. Variables selected for the best-fit model are discussed in terms of the host selection behavior of *P. quercivorus*.

Materials and methods

Site description and field measurements

This study was conducted in a secondary forest around a bog in Hacchodaira, in the eastern part of Kyoto Prefecture, Japan (Fig. 1a). The forest is dominated by two

Fagaceae species, *Q. crispula* and *C. crenata*, which are the known hosts of *P. quercivorus*. In this 93-ha area (Fig. 1b), trees killed by *P. quercivorus* were first observed in 2008, and trees attacked by *P. quercivorus* from 2008 to 2011 were observed in the field. These observations were made in the year of attack that followed the start of the current year's attack (for instance, trees attacked in 2008 were examined from April to June 2009) by checking for beetle holes bored in the lower part of the tree and frass ejected from the holes. < Fig. 1

Three plots were established in the study forest: Plots A and B, 1 ha each; and Plot C, 0.5 ha (Fig. 1b, 2). These plots were located at an altitude ranging from 820 m to 920 m. From 2010 to 2012, the specific location of each *Q. crispula* and *C. crenata* tree >10 cm diameter at breast height (DBH) in the study plots was determined using differential GPS (GENEQ, SXBlue II) and laser rangefinder with compass (Laser Technology, TruPulse 360B). Crown projections were made for each tree using the same apparatus. To examine differences in tree size among plots and between species, two-way analysis of variance (ANOVA) was conducted using the *stats* package of R 2.15.3 (R Core Team, 2013).

< Fig. 2

Preparation of variables

To evaluate the effect of tree size on the probability of attack by *P. quercivorus*, the basal area (BA) of each tree was calculated from the DBH. In the case of multi-stemmed trees, the BA of all stems was summed. Altitude (ALT), slope angle (SLOPE), and profile curvature (PCURV) at the location of each individual tree were calculated from a digital elevation model provided by the Geospatial Information Authority of Japan to assess the effects of these topographic features on the probability of beetle attack. These calculations were performed using GRASS geographic information system (GIS) software (GRASS Development Team, 2010).

We presumed that the surrounding density of potential host trees would affect the probability that an individual tree would be attacked by the beetle, but the scale of this effect was unknown. Moreover, the ways in which density could affect the probability of attack could differ according to area. For example, the "dilution effect" of a large but dispersed number of potential host trees might come into play at large spatial

scales, while the density of potential host trees within a small area could be positively correlated with the probability of beetle attack. It is also probable that a high density of potential host trees would have a positive effect on beetle attack at large spatial scales. To examine this point, we prepared a density variable (DE) by generating buffers around each stem using 11 different scales at 2.5-m intervals from a 0- to 25-m radius, and the sum of the number of *Q. crispula* and *C. crenata* stems included in each buffer. The number of stems within a 0-m radius referred to the number of stems of individual trees that ramified at the base (below 1.3 m above ground). When the generated buffer crossed the boundary of the study plot, DE was corrected by dividing the number of stems by the proportion of the buffer area inside the study plot in relation to the total buffer area. We prepared 55 pairs of variables from these 11 DEs. Each pair included a variable DE1: the number of stems within a given concentric area; and a variable DE2: the number of stems within a given concentric area outside of DE1 (Fig. 3). Trees killed by beetle attacks in the previous year were eliminated from these calculations. < Fig. 3

The crown density of potential host trees was also a candidate explanatory variable for predicting the probability of beetle attack. Crowns of *Q. crispula* and *C. crenata* were converted from vector to raster with 0.5-m resolution (200 × 200 cells for a 1-ha plot) using GRASS GIS software. The crown-density variables (CRs) were prepared by generating buffers around each stem using the 11 scales defined above, and the sum of the number of crown layers in each cell was included in each buffer. The number of crown layers within a 0-m radius refers to the number of crown layers of the raster cell directly above an individual tree. The crown densities of trees killed by beetle attack in the previous year were eliminated from these calculations. CR calculated for the largest scale was approximately 5000 times greater than CR calculated for the smallest scale, and incorporation of such a large explanatory variable into the model would cause failure in convergence. Therefore, the CR values calculated for each scale were standardized before model construction.

Model selection

We modeled the probability of a tree being attacked by *P. quercivorus* using a generalized linear mixed model (GLMM) with the *lme4* package of R 2.15.3 (R Core

Team, 2013). The response variable used in the model was the proportional data of the number of stems that were attacked within an individual tree. For example, when 2 of a tree's 4 stems were attacked (proportion of attacked stems = 0.5), the data (attacked, attacked, non-attacked, non-attacked) were assumed to follow a binomial distribution with 4 trials. If the same proportion of stems was attacked (0.5) in a tree with a different number of stems, the data were assumed to follow a binomial distribution with the number of trials equal to the total number of stems. Because the response variable followed a binomial distribution, we set the link function of the model as the logit link. Candidate explanatory variables were tree species (SP), BA, previous infestation history, ALT, SLOPE, PCURV, a pair of DE variables calculated for two different scales (DE1 and DE2), and the CR of fagaceous trees. The year (2008, 2009, 2010, or 2011) and the plot (A, B, and C) in which beetle attack occurred were included in the model as random intercepts, because the probability of attack was likely to be correlated among trees in the same year or site.

By changing the combination of DE1, DE2, and CR, 605 models were constructed. Each model included SP, BA, previous infestation history, ALT, SLOPE, PCURV, any one pair of DE1 and DE2 values, and one of 11 CR values as explanatory variables. Among these 605 models, the model with the lowest Akaike's information criterion (AIC) was selected as the full model. At this stage, Pearson's correlation coefficients (r) among continuous variables (BA, ALT, SLOPE, PCURV, DE1, DE2, and CR) were calculated to identify and exclude highly correlated ($|r| \geq 0.6$) variables. No variables were highly correlated, and thus none were excluded from the analysis. The best-fit model was sought from the full model by comparing the AIC of 512 candidate models with various combinations of the 9 explanatory variables. The relative variable importance (RVI) of each candidate explanatory variable was calculated using Akaike weights for these 512 models. Comparison of AIC and calculation of RVI were performed using the *MuMIn* package of R 2.15.3 (R Core Team, 2013).

Results

The number of individuals and the basal area of *Q. crispula* and *C. crenata* in each plot are shown in Table 1. Generally, the basal area of *C. crenata* was larger than

253 that of *Q. crispula* (two-way ANOVA, $F = 5.676$, $P = 0.0178$). The combined basal
254 area of *Q. crispula* and *C. crenata* in Plot C was smaller than that in Plot A, although
255 the difference was not significant (two-way ANOVA, $F = 2.668$, $P = 0.0711$). Table 2
256 shows the proportion of *Q. crispula* and *C. crenata* stems that were attacked each year,
257 in each plot. In general, a greater proportion of *Q. crispula* stems was attacked than *C.*
258 *crenata*, except for Plot B in 2008 and Plots A and C in 2009 (Table 2). With the
259 exception of *Q. crispula* in 2008, the proportion of stems attacked in Plot C was lower
260 than that in Plots A and B (Table 2). In total, 291 fagaceous trees were observed in the
261 three plots (Table 1). From 2008 to 2010, 50 individuals were killed by *P. quercivorus*
262 attack. We constructed a model to predict the probability of beetle attack occurring on a
263 particular tree in each of the four years (2008, 2009, 2010, and 2011), resulting in a total
264 of 1134 samples (291 × 4 – 50). < Tables 1,2
265 Among the 605 candidate models, the model including DE1 (5 m), DE2
266 (5–17.5 m), and CR (2.5 m) as explanatory variables had the lowest AIC value, and
267 further model selection was performed by setting this as the full model. Correlation
268 coefficients among BA, ALT, SLOPE, PCURV, DE1 (5 m), DE2 (5–17.5 m), and CR
269 (2.5 m) are shown in Table 3. The strongest positive correlation (0.335) was observed
270 between ALT and SLOPE, and the strongest negative correlation (-0.385) was observed
271 between BA and DE2, although all coefficients were within the range of weak or low
272 correlation (Table 3). Therefore, no variables were excluded from the model. < Table 3
273 Results of the best-fit model are shown in Table 4. Tree species, previous
274 infestation history, DE1 (5 m), DE2 (5–17.5 m), and CR (2.5 m) were included as
275 explanatory variables; the remaining variables were excluded from the model (Table 4).
276 The predicted probability of attack calculated for various combinations of DE1 (5 m) < Table 4
277 and DE2 (5–17.5 m) is shown in Fig. 4. Probability of attack increased with increasing
278 values of DE1 when DE2 was held constant, and with decreasing values of DE2 when
279 DE1 was held constant. The highest probability of attack was predicted when the target
280 tree was surrounded by many other fagaceous trees within a 5-m radius of its location
281 and when no other fagaceous trees were present within a radius from 5 to 17.5 m from
282 its location (see top left of Fig. 4). The lowest probability of attack was predicted when
283 the target tree was the only individual within a 5-m radius and when many other

fagaceous trees were present within a radius from 5 to 17.5 m from its location (see bottom right of Fig. 4). < Fig. 4

Discussion

The probability that *Q. crispula* would be attacked by *P. quercivorus* was higher than that for *C. crenata* when the effect of the other explanatory variables was held constant (Table 4). This finding is consistent with that of a previous study that showed *P. quercivorus* preferred *Q. crispula* over *C. crenata* as its host at the stage prior to hole boring (Yamasaki & Futai, 2012). The proximate cause of this preference for *Q. crispula* is unclear; however, the ultimate cause of the selection was suggested by Tarno *et al.* (2011), who showed a higher reproductive success of *P. quercivorus* on *Q. crispula* than on *C. crenata*.

Trees attacked in the previous year had a lower probability of being attacked by *P. quercivorus* when the effect of the other explanatory variables was held constant (Table 4). Previous research has shown that the probability of a male beetle flying to a tree was not affected by the tree's previous infestation history, but that the probability of the beetle boring a hole into a tree was negatively affected by the tree's previous infestation history; these findings suggest that *P. quercivorus* approaches trees irrespective of their infestation history, but that after the approach it flies away from those with a history of infestation (Yamasaki & Futai, 2008). Urano (2000) reported that no beetles emerged successfully from trees that had survived previous attack, and suggested that trees with a history of infestation were resistant to *P. quercivorus*; this resistance could be the ultimate cause of the beetles' aversion to previously infected trees.

As we hypothesized, the stem density of potential host trees had an effect on the probability of attack by *P. quercivorus*, and the way in which density affected this probability differed according to spatial scale. Stem density had a positive effect on the probability of attack at smaller scales, and a negative effect at larger scales (Table 4). The positive effect at the small scale suggested that the beetle is attracted by stems aggregated within a radius of approximately 5 m, which could be explained by the enhanced probability of finding the host at this scale. At this small scale, trees distributed in clumps (see left side of Fig. 4) had a higher probability of attack than

316 trees that were the only individual within the 5-m radius (see right side of Fig. 4).
317 However, this attracting effect was reduced when host trees were densely distributed in
318 the surrounding larger area. The negative effect at larger scales suggested a “dilution
319 effect,” in which stems are more dispersed and the probability of an individual tree
320 being attacked may decrease as the number of attack targets increases. In an original
321 definition of the dilution effect from behavioral ecology, this effect occurs when attack
322 rate does not increase proportionately with group size (Davies *et al.*, 2012). The
323 population density of *P. quercivorus* might not be sufficiently high to overcome this
324 dilution effect. This study was conducted in a forest at the initial stage of *P.*
325 *quercivorus*-induced mass mortality. An increase in the population density of *P.*
326 *quercivorus* at a later stage may change the way in which host-tree density affects the
327 probability of attack. Although the effect of the surrounding density of potential hosts
328 has been described previously for *P. quercivorus* (Yamasaki & Sakimoto, 2009) and
329 other beetles (Perkins & Roberts, 2003; Negrón & Popp, 2004; Coops *et al.*, 2006;
330 Negrón *et al.*, 2008; Negrón *et al.*, 2009; Santos & Whitham, 2010), the present study is
331 the first to show different effects of density according to spatial scale.
332 The increasing probability of attack by *P. quercivorus* with increasing CR within
333 a small (2.5 m) radius around individual trees suggests that the beetle has a means of
334 detecting areas with high crown density. Crown density is thought to be independent of
335 DE in areas with high slope angles, and there were no significant correlations between
336 CR and DE in our study (Table 3). Therefore, the effect of CR was also considered
337 separately from the effect of DE. The genus *Quercus* is known to exhibit high emission
338 rates of volatile organic compounds (VOC) (Isebrands *et al.*, 1999; Guenther *et al.*,
339 1994); VOCs emitted from fagaceous trees may enable beetles to detect their target
340 hosts from above. The flying activity of *P. quercivorus* above the canopy must be
341 examined to verify this hypothesis.
342 Basal area was not included in the best-fit model for predicting the probability of
343 attack by *P. quercivorus* (Table 4), suggesting that the beetle showed no preference
344 according to tree size. This result contrasts with those of recent studies that showed *P.*
345 *quercivorus* preferred thicker trees as its attack target (Akaishi *et al.*, 2006; Yamasaki &
346 Sakimoto, 2009). Yamasaki and Sakimoto (2009) investigated factors affecting the
347 probability of *P. quercivorus*-induced mortality of *Q. crispula* in a natural forest with a

large variability in tree size (BA from 80 to 14420 cm^2) and detected an effect of this parameter. The present study was conducted in a secondary forest in which tree basal area varied from 50 to 4970 cm^2 (Table 1); it is possible that *P. quercivorus* might not show a preference within this narrow range of area. In addition, we analyzed the probability of an initial beetle attack, not the probability of mortality after the occurrence of a mass attack. A preference for thicker trees may develop in *P. quercivorus* after the initial attack phase, i.e., at the mass attack phase.

An alternative explanation for the disagreement among results with regard to tree size lies in differences among the study plots. Although the difference was not significant, *Quercus crispula* trees in Plot C were smaller than those in Plots A and B (Table 1), and the proportion of stems of *Q. crispula* attacked in Plot C was lower than that in Plots A and B, except for in 2008 (Table 2). We treated plot as a random effect in the model because it was thought that some unmeasured variables (e.g., distance from sites that were heavily infested in previous years) would be present that would differ among plots. Therefore, any difference in the probability of attack resulting from differences in tree size may have been masked by assigning plot as a random effect.

In this study, no topographic parameters (i.e., ALT, SLOPE, PCURV) were selected as explanatory variables for predicting attack by *P. quercivorus* (Table 4). A previous study conducted at 20 sites with altitude ranging from 120 to 860 m showed a negative effect of altitude on the probability of attack by *Platypus* beetles on *N. cunninghamii*; this effect was explained by decreased beetle activity at lower temperatures (Elliott *et al.*, 1987). The altitude of our study site ranged from 820 to 920 m, and this range may be too narrow for detecting an effect. Further, the present study analyzed the probability of initial attack, not the probability of mortality as a result of reproductive activity and growth of the beetle inside sapwood. Reproduction and growth of *P. quercivorus* may be indirectly affected by altitude via effects of altitude on tree physiological status; however, the beetle's host-detection behavior may not be affected by topographies in the initial phase of attack. To clarify this point, analysis of the probability of mortality caused by *P. quercivorus* must be performed using only the data on attacked trees.

A possible host selection process for *P. quercivorus* suggested by the results of this study can be summarized as follows. First, beetles locate a cluster of host trees from

above by detecting areas with high crown density of the host. After finding a cluster, the insects descend from the canopy, circling around the cluster of host trees. At this stage, if the initial target cluster is relatively small in size, beetles switch to other clusters of fagaceous trees close to the initial target. Among a cluster of host trees, they narrow the target to the stem of a susceptible tree species and land on the bark surface. Finally, *P. quercivorus* accepts a tree with no infestation history as its host.

Igeta *et al.* (2004) suggested that the majority of *P. quercivorus* traveled in lower strata of the forest, and that only a small proportion of the beetles flew at the top of the forest canopy; however, the flight behavior of *P. quercivorus* at its dispersal stage has not been elucidated in detail. Questions remain as to which direction this beetle flies after emergence from holes bored in the host trees, the height at which it flies when searching for a new host tree, and the direction from which it approaches a new host tree. Further field studies are necessary to clarify these points.

In Japan, coppices of fagaceous trees were maintained for fuel wood in the past. Conversion of fuel sources from charcoal and wood to gas and electricity occurred in the 1960s (the fuel revolution), and after that, abandoned coppices matured into secondary forest with densely distributed, multi-stemmed fagaceous trees, although these species generally grow as single stems and do not dominate forests under natural conditions. Kobayashi and Ueda (2005) suggested that the dense distribution of multi-stemmed trees is a cause of recent Japanese oak wilt. Our finding, that high stem density on small scales had a positive effect on the probability of attack by *P. quercivorus*, is consistent with this suggestion. Therefore, sustainable use of fagaceous trees such as was practiced before the fuel revolution may help to reduce damage by *P. quercivorus*. The effectiveness of thinning as a defense against bark beetle attack was demonstrated for ponderosa and lodgepole pine stands (reviewed in Fettig *et al.*, 2007).

Our results also showed that, at small scales, densely distributed fagaceous trees had a higher probability of attack when they were isolated from other clumps of related trees at larger scales. This situation corresponds, for example, to forest edges where trees are exposed to open areas on at least one side. In the field, *P. quercivorus* was captured at forest edge areas in high frequency (Igeta *et al.*, 2003). The beetles may easily discover host trees at forest edges without interference from information (e.g., VOC signals) from other tree species. In situations in which it is not possible to protect

412 all potential host trees from beetle attack, priority must be placed on protecting trees on
413 the forest edge.

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415

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561 **Table 1.** Number of individuals and basal area (mean ± standard deviation) of *Quercus*
562 *crispula* and *Castanea crenata* in each plot
563

	Q. crispula		*C. crenata*	
	Number of individuals	Basal area of individuals (m^2)	Number of individuals	Basal area of individuals (m^2)
Plot A	43	0.124 ± 0.067	56	0.153 ± 0.093
Plot B	37	0.111 ± 0.101	74	0.124 ± 0.080
Plot C	38	0.098 ± 0.077	43	0.128 ± 0.077

564

565 **Table 2.** Proportion of *Quercus crispula* and *Castanea crenata* stems attacked by
566 *Platypus quercivorus*. Numbers in parentheses indicate number of attacked stems and
567 number of stems present at the beginning of the year in each plot.
568

	2008		2009		2010		2011	
	Q. crispula	*C. crenata*	*Q. crispula*	*C. crenata*	*Q. crispula*	*C. crenata*	*Q. crispula*	*C. crenata*
Plot A	0.189 (10/53)	0.152 (10/66)	0.038 (2/52)	0.045 (3/66)	0.098 (5/51)	0.045 (3/66)	0.196 (9/46)	0.031 (2/65)
Plot B	0.048 (3/62)	0.094 (8/85)	0.048 (3/62)	0.037 (3/82)	0.177 (11/62)	0.037 (3/82)	0.230 (14/61)	0.062 (5/81)
Plot C	0.052 (3/58)	0 (0/45)	0 (0/56)	0 (0/45)	0.054 (3/56)	0.022 (1/45)	0.041 (2/49)	0.022 (1/45)

569

570 **Table 3.** Pearson's correlation coefficients for each candidate explanatory variable for a
571 model to predict the probability of attack of *Quercus crispula* and *Castanea crenata* by
572 the ambrosia beetle, *Platypus quercivorus*
573

	BA		ALT		SLOPE		PCURV		DE1		DE2	
ALT	0.015											
SLOPE	0.049		0.335	***								
PCURV	-0.160	***	-0.082	**	-0.279	***						
DE1	-0.181	***	-0.029		-0.092	**	0.137					
DE2	-0.385	***	-0.295	***	-0.186	***	0.290	***	0.198	***		
CR	-0.019		0.135	***	0.029		0.213	***	0.248	***	0.173	***

574

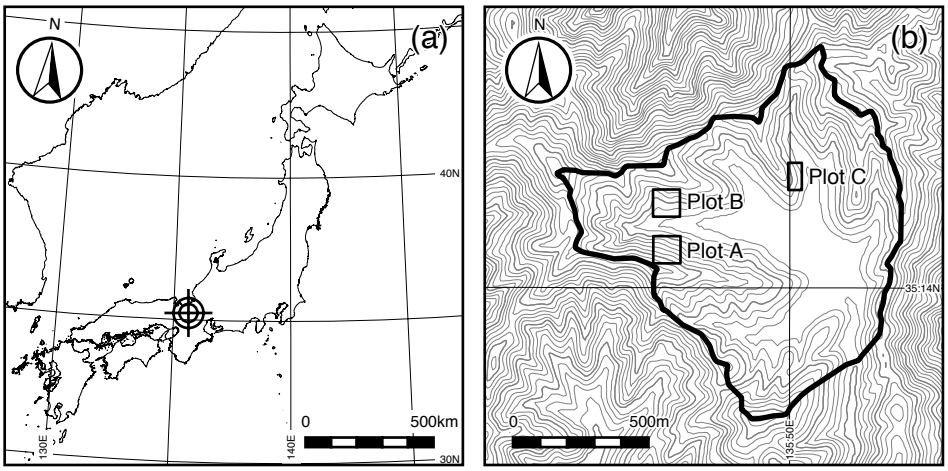
575 BA = basal area of each tree
576 ALT = altitude at the location of each tree
577 SLOPE = slope angle at the location of each tree
578 PCURV = profile curvature at the location of each tree
579 DE1 = number of *Q. crispula* and *C. crenata* stems within a 5-m radius
580 DE2 = number of *Q. crispula* and *C. crenata* stems within the 5- to 17.5-m radius
581 surrounding DE1
582 CR = cumulative value of the number of crown layers in each 0.5 × 0.5-m cell, within
583 a 2.5-m radius
584 ** $P < 0.01$, *** $P < 0.001$
585

586 **Table 4.** Results of a generalized linear mixed model that predicted the probability of
587 attack of *Quercus crispula* and *Castanea crenata* by the ambrosia beetle, *Platypus*
588 *quercivorus*. Estimated coefficients, their standard errors, and *z*-statistics are shown.
589 Variables without estimates were not selected as explanatory variables for the best-fit
590 model. The number of trees (n) used in the model was calculated as follows: 291 trees x
591 4 years of study – 50 trees killed by *P. quercivorus*; n = 1134.
592

Predictor variable [a]	Estimate	SE	*z*	*P* [b]		RVI [c]
SP	0.9619	0.2235	4.303	< 0.0001	***	1.00
Infestation history	- 1.2117	0.4668	- 2.596	0.0094	**	0.97
DE1 (5 m)	0.1856	0.0663	2.799	0.0051	**	0.94
DE2 (5–17.5 m)	- 0.0674	0.0174	- 3.874	0.0001	***	0.99
CR (2.5 m)	0.4668	0.1235	3.780	0.0002	***	1.00
BA	-	-	-	-		0.45
ALT	-	-	-	-		0.35
SLOPE	-	-	-	-		0.28
PCURV	-	-	-	-		0.37

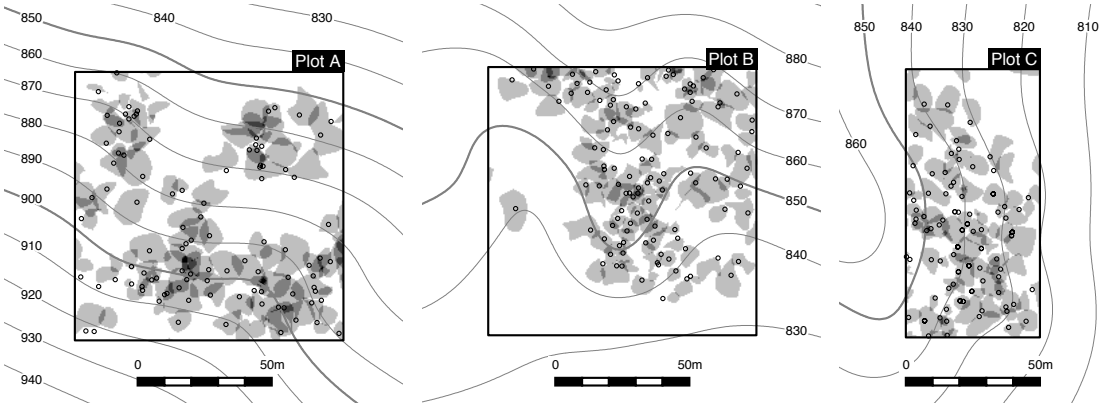
593
594 [a] SP = tree species attacked by *P. quercivorus* (showing the estimated intercept for
595 *Quercus crispula* when *Castanea crenata* is set as a baseline)
596 Infestation history = infected or not infected by *Platypus quercivorus* in preceding
597 years (negative value of the estimate indicates the negative effect of infestation
598 history on the probability of attack)
599 DE1 (5 m) = number of *Q. crispula* and *C. crenata* stems within a 5-m radius
600 DE2 (5–17.5 m) = number of *Q. crispula* and *C. crenata* stems within the 5- to 17.5-m
601 radius surrounding DE1
602 CR (2.5 m) = cumulative value of the number of crown layers in each 0.5 × 0.5-m cell,
603 within a 2.5-m radius
604 BA = basal area of each tree
605 ALT = altitude at the location of each tree
606 SLOPE = slope angle at the location of each tree
607 PCURV = profile curvature at the location of each tree
608 [b] Significance of differences from zero tested using *z*-statistics (** $P < 0.01$, *** $P <$
609 0.001)
610 [c] Relative variable importance calculated using Akaike weights of all candidate models

611 **Fig. 1.** (a) Location of the study site, Hacchodaira, in Japan. (b) Locations of three plots
612 established in the study site. The area surrounded by the thick black line indicates the
613 93-ha area in which fagaceous trees attacked by *Platypus quercivorus* were surveyed.
614



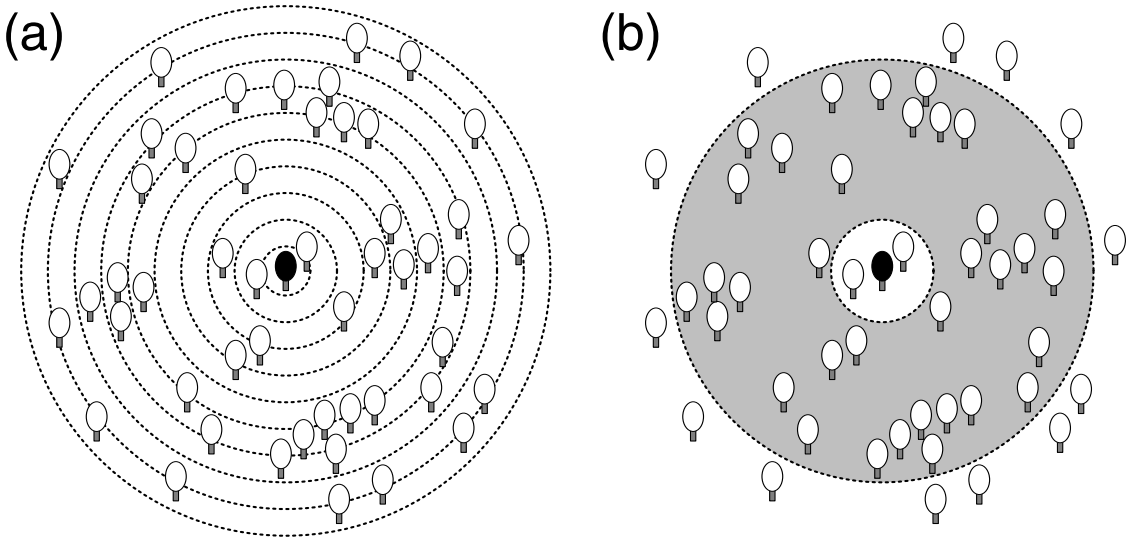
615

616 **Fig. 2.** Distribution of *Quercus crispula* and *Castanea crenata* in three plots established
617 in a secondary forest of Hacchodaira, Japan. Open circles show the locations of
618 individual trees; gray areas indicate the crown area of each tree. Overlapped crowns are
619 shown in darker gray. Numbers on the contour lines indicate altitude (m).
620



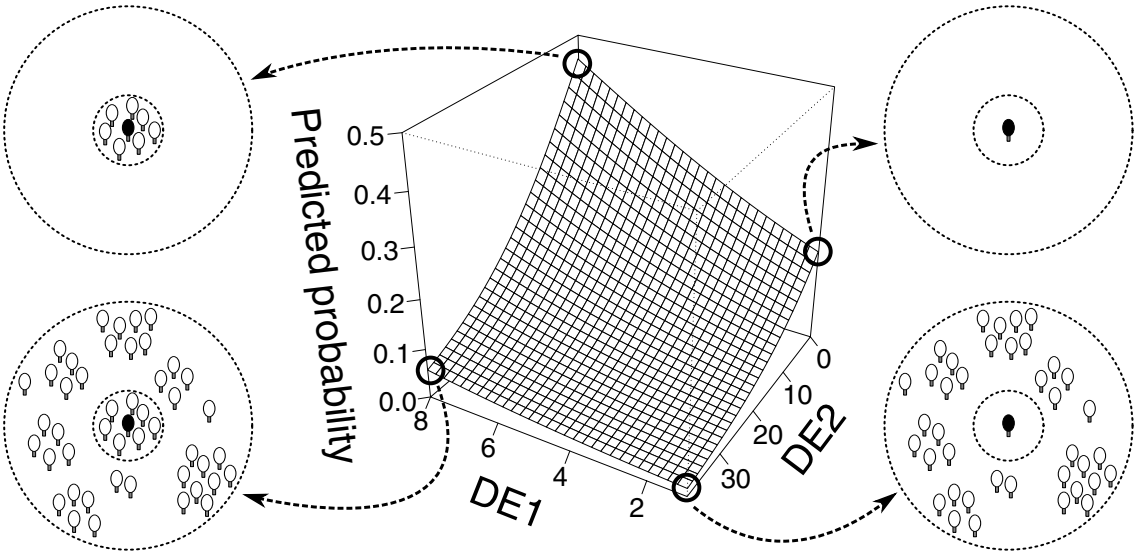
621

622 **Fig. 3.** Preparation of density variables (DE). (a) Buffers were generated around each
623 *Quercus crispula* and *Castanea crenata* stem using 11 different zones at 2.5-m intervals.
624 (b) Fifty-five pairs of DE variables: the number of stems within a given radius (white
625 circular area, DE1) and the number of stems in the surrounding area (gray area, DE2),
626 were calculated by varying the size of the buffer. In this figure, DE1 (e.g., 0–5 m) = 3
627 stems and DE2 (e.g., 5–20 m) = 34 stems.
628



629

630 **Fig. 4.** Probability of *Quercus crispula* being attacked by *Platypus quercivorus*
631 predicted by a generalized linear mixed model. DE1 (number of *Q. crispula* and
632 *Castanea crenata* stems within a 5-m radius) and DE2 (number of *Q. crispula* and *C.*
633 *crenata* stems within the surrounding 5- to 17.5-m radius) are changed sequentially
634 within the range of data used for the model construction. To calculate the probability of
635 attack, previous infestation history was set to zero (no infestation history) and CR
636 (cumulative value of the number of crown layers within a 2.5-m radius) was set to its
637 average value. Illustrations of trees show scenarios for 4 combinations of DE1 and DE2,
638 with their lowest or highest values. The probability of attack was predicted for trees at
639 the center of the circles (black trees).
640



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